Adaptations of Andean and Tibetan birds: a brief comparison[1]

JEAN DORST

National Museum of Natural History, Paris

The Andes and Tibet—the Roof of the World—are the most formidable and extensive mountain assemblages of the world. Both constitute temperate or cold plateaux over which rise very high mountains surrounded by tropical or semi-tropical warm habitats at least for a part. Animals which succeeded the colonization of these regions had to adapt not only to altitude, but to its ecological consequences, particularly a harsh climate and a scarce vegetal cover.

Of course conditions differ to a great extent in both areas, above all in consequence of the different latitudes under which they lie. The high Andes from Colombia to Peru are located within the intertropical zone, whereas Tibet has a more northern situation and its northern border is contiguous to cold regions. Nevertheless, as many ecological features are similar, it is worthwhile to compare the evolution and convergent ecological adaptations of the Andean and of the Tibetan avifaunas.

Comparisons can also be made with the high mountains of Africa, though the African montane habitats merely constitute small 'islands' isolated amidst warm tropical lowlands. In spite of their very specialized fauna, they are not similar to the other high mountains in regard to speciation and faunal differentiation. Ethiopia is the only part of Africa where corresponding geographical conditions occur, as there is an extensive highland area, but average altitude is lower and birds have to face less severe ecological factors.

This paper mostly refers to the Northern plateau of Tibet (Chang Tang) and to the high Andes of Ecuador and Peru (the Chilean sector differs widely by its climate and ecological conditions), and mentions only briefly the African mountains. It considers only a few of the adaptations of birds established in the upper zone, above about 4000 m. where open habitats are largely dominant.

In both areas, climate is very harsh. In the Andes, mean temperatures are relatively low, the annual mean temperature averaging 1-2°C in the region of lake Titicaca. There is a wide daily range, sometimes

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from −15°C at night to +15°C and more during the day. The northern sector is humid, due to high rainfall, well distributed through a good part of the year. The southern sector is much drier, as rainfall is concentrated during the austral summer and as the dry season is long and very severe; dryness and cold are exaggerated by strong winds. There is no snow under 4000 m, except during brief storms, after which it rapidly melts.

In the part of Tibet considered here, climate is still more severe. Temperatures are very low, and may fall well below freezing during any part of the year (temperatures of −44°C have been recorded). Rains are restricted to a short period during the summer. Thus dryness is an important feature, accentuated by strong and almost permanent winds. Snow may cover the soil for long periods, even in summer. Climatic conditions are definitely more severe than in the Andes, particularly in winter, due to cold and snow.

It is not surprising that such conditions strongly influenced the vegetal cover. Arboreal vegetation is absent from the upper level, except in a very few places. Grassy alpine steppes predominate across flat expanses, valley beds or plateaux, formed of coarse tufts of Gramineae between which grow a small variety of herbaceous plants and sparse bushes. Shrubs and other ligneous plants only grow in sheltered places, close to cliffs or on well exposed slopes. Beyond a certain altitude, around 5000 m, but varying according to local conditions, the landscape is barren and rocky habitats maintain the last vestige of vegetation.

Birdlife reaches the limits of permanent snow. In the Andes, various birds such as *Thinocorus orbignyianus*, *Cinclodes fuscus*, *Geositta cunicularia* and even hummingbirds such as *Patagona gigas* are observed up to 5000 m. In Tibet *Pyrrhocorax graculus*, *Grandala coelicolor* *Prunella collaris* and *Carpodacus puniceus* commonly live at elevations of 5700 m. Practically birdlife ends at the upper limit of vegetation. But birds were recorded at much higher altitudes, particularly in Tibet, where *Anthus novaeseelandiae*, *Phoenicurus ochruros*, *Columba rupestris*, *Corvus corax*, *C. macrorhynchos*, *Upupa epops* and *Prunella collaris* were observed at well over 6000 m, and *Pyrrhocorax graculus* at 8229 m ; geese have been reported as flying at a height above that of Mt Everest (8847 m) during migrations (quoted by Vaurie 1972). Apparently they live with perfect ease in spite of the incredible effort needed just to fly.

Evolution and speciation

It is needless to say that the avifaunas of these two regions differ fundamentally by their origin and that they have no relationship, except a few ubiquitous birds represented in each area by allied species. The

Andean avifauna derives from stocks which emigrated from the surrounding lowlands or from Patagonia from where a series of birds spread northwards. The avifauna of Tibet, and particularly of the part concerned, is chiefly of Palearctic origin, though a few Sino-Himalayan elements penetrated even the Chang Tang (7 species according to Vaurie 1972). In spite of different origin, birdlife shows some astonishing convergences and parallelisms in evolution due to identical factors of the environment to which they had to adapt.

Both avifaunas are greatly impoverished when compared to those of nearby lowlands. Climate acted as an efficient filter and eliminated a large number of potential colonizers, particularly those which are partial to closed habitats. The upper Andes are inhabited by 153 species, aquatic birds excluded (Vuilleumier), and the northern plateau of Tibet by 175, among which only 67 are found on the Chang Tang. Both avifaunas are more diversified than their African counterpart. In Africa only 74 species are met in the montane non-forest zones, which due to its limited surface, have never been active centres of differentiation in contrast to the forests which surround them (Moreau 1966).

In the Andes and in Central Asia, very active adaptative radiation occurred in relation to isolation. Andean 'islands' conform to archipelagos in many ways, in spite of some differences (Vuilleumier 1970). Though adaptative radiation interferes with geographic speciation, which also reaches a very high degree in mountains as a consequence of discontinuity of ranges and variety of habitats, lack of competition due to the limited number of original stocks favoured differentiation of sympatric species occupying various niches. In the Andes this phenomenon affects particularly Furnariidae (*Geositta*, *Upucerthia*, *Cinclodes*, *Asthenes*), Tyrannidae (*Muscisaxicola*) and Fringillidae (*Spinus*, *Sicalis*, *Phrygilus*).

In Tibet, adaptative radiation occurs among Turdidae (*Phoenicurus* is represented by 9 of its 11 species), Fringillidae (*Carpodacus*, with 14 of the 17 species of the Old World; *Rhodopechys*, with 3 of the 4 species of the genus) and Ploceidae (*Montifringilla*, with 6 of the 7 species of the genus, 4 being endemic ; ecological differentiation is particularly visible among Snow Finches, each species being adapted to a well defined habitat). It is worthwhile to note that granivorous birds radiated intensively, probably in relation to the diversity and the large amount of seeds available in these habitats. The Andes and Tibet have been very important evolutionary centres, a fact also attested by the number of characteristic species, endemic or having secondarily spread over larger areas.

In contrast adaptative radiation did not occur in the montane non-forest zones of Africa, even in Ethiopia, probably as a consequence of the limited areas involved.

Parallel evolution

In spite of their completely different origin, the Andean and the Tibetan faunas show striking parallelisms. Homologous species differentiated in the same type of habitat, due to similarities of available ecological niches. In a very few cases, they belong to the same genus. Thus pipits of the genus *Anthus* nest on the high Andean plateaux (*A. correndera*, *A. furcatus*, *A. bogotensis*) and in Tibet (*A. roseatus*), apparently in the same type of habitat. Many raptors, such as representatives of the genera *Buteo* and *Bubo* and grebes (*Podiceps*) are found in both areas, where they occupy the same niches. But in most cases, birds originate from very different stocks and show remarkable convergences. In Tibet, Snowcock *Tetraogallus tibetanus* peculiar to stony habitats, Partridges *Perdix hodgsoniae*, and Sandgrouse *Syrrhaptes tibetanus* peculiar to grassland, occupy somewhat the niche filled in the Andes by various tinamous, and maybe also by Seedsnipes *Thinocorus orbignyianus*. Several Tibetan larks (*Calandrella cinerea*, *C. acutirostris*, *Eremophila alpestris*, *Melanocorypha maxima*) and wheatears (*Oenanthe deserti*) are the ecological equivalents of various Andean Furnariidae, particularly representatives of the genera *Geositta* and *Upucerthia*, many of which show similar morphology, pattern and even behaviour. Many similitudes also exist among seedeaters, well represented in both areas. In the Andes, birds belonging to the genera *Phrygilus*, *Sicalis*, *Spinus* and *Zonotrichia* are well diversified and their populations abundant through most of the habitats, particularly in grasslands which cover extensive surfaces on the altiplano. In Tibet, birds of the genera *Montifringilla*, *Acanthis*, *Leucosticte* and *Carpodacus* occupy the same niches and are just as numerous. Among insectivores, *Phoenicurus* can in some way be considered as the equivalent of various Tyrannidae, such as *Muscisaxicola* and *Ochtoeca*.

It can be admitted that at least at some levels, the Andean and the Tibetan ecosystems have the same structure and that birds of different origins play the same role in the ecology of these two regions. In contrast there are differences, due to geographical and ecological features. Aquatic avifauna is well diversified on the Andean high plateaux in relation to the wealth of lakes and wetlands. A series of ducks (*Anas flavirostris*, *A. puna*, *A. spinicauda*, *A. specularioides*, *Oxyura ferruginea*), grebes (*Podiceps rolland*, *P. occipitalis*), coots (*Fulica americana*, *F. gigantea*), Ardeiformes (*Plegadis ridgwayi*, *Nycticorax nycticorax*) and some waders colonized various aquatic habitats where their populations are often numerous. They have no equivalent on the Tibetan plateaux where the breeding Anseriformes are mostly *Aythya nyroca*, a scarce bird, and *Mergus merganser*, a characteristic bird of the highlands from 4000 to

4700 m, avoiding the lower elevations during the breeding season. Except *Anser indicus*, *Tadorna ferruginea* and a few ducks, the other Anseriformes met on the northern plateau of Tibet are mostly migrants or stragglers.

Among other aquatic birds, grebes and gulls nest in both regions, *Larus serranus* in the Andes and *L. brunnicephalus* in Tibet, where common terns *Sterna hirundo* also nest up to 4800 m, without equivalent in the Andes. Waders, present in both regions, at least as migrants, are more diversified in Tibet where several nest, among which *Charadrius mongolus*, up to 5100 m, the Redshank *Tringa totanus*, *Gallinago solitaria*, up to 4500 m (its Andean counterpart is *G. paraguaiae*), and the Ibisbill *Ibidorhyncha struthersi*, a bird strictly adapted to streams.

Broadly speaking, though the Tibetan avifauna comprises a few birds with no Andean equivalent, aquatic communities seem much less flourishing in Tibet than in the Andes, maybe in relation to lower productivity of the adequate biota and to severe winter conditions, though the latter might be overcome by seasonal movements.

In each area other birds are found with no equivalent in the other for both faunistic and ecological reasons. Thus the Andean hummingbirds (*Oreotrochilus*, *Chalcostigma*, *Patagona*) have no counterparts, no sunbird being adapted to high elevations. In contrast, some Tibetan birds such as the crane *Grus nigricollis* and corvids have no Andean equivalents.

Nevertheless, the avian communities of the two regions show remarkable convergences. When the same niche is available in both areas it is occupied by birds from different origin, but which evolved with some parallelism. Birds exploit the same type of resources, and concentrate at the same trophic levels. Vegetarians are numerous and insectivores are present, though not the dominant group. Most of them are specialized feeders and many are polyphagous. Raptors also are numerous and well diversified, particularly in Tibet, many of them preying on rodents. These mammals play a very important role in the high mountain ecosystems, as converters of vegetal to animal matter, being abundant and much diversified. Many of them are active in daytime, probably as a response to nocturnal coldness. Therefore they can be preyed on by many raptors, such as buzzards, the diet of which is largely made up of these mammals.

It should be stressed that vultures are numerous in Tibet, just as they are in the high mountains of Africa, particularly in Ethiopia, whereas their Andean counterparts are scarcer and less diversified. This could be related to the fact that larger mammals are much more diversified in the Old World than in the Neogea. Therefore large scavengers could not find a suitable niche in the Andean habitats where the only indigenous ungulates are Auchenidae and a few deer.

Ecological adaptations

In both regions, birds had to overcome many difficulties to colonize the upper zones. The few which succeeded had to adapt to very hostile environments, not only to altitude in itself, but also to its climatic consequences. As a response to low oxygen pressure they developed anatomical and physiological mechanisms, probably the same in all areas of high elevation over the world. Other adaptations are of ecological nature, and probably these are even more important to the birds. Remarkable convergences are found when birds from the Andes and from Tibet are compared.

Birds are not evenly distributed over these bleak regions, but concentrate in the most favourable places. Therefore their distribution is largely discontinuous and their populations split into small units, sometimes separated over great distances by unsuitable habitats (this had a consequence on speciation, definitely favoured by such distribution). As birds had to concentrate within small areas, many became gregarious. In the Andes, many birds show a strong tendency to gregariousness, at least during the non-breeding season. Many passerines, such as Fringillidae, gather during the night in sheltered places, under rocks or in crevices, which provide roosts and better refuges against cold and bad weather. During the breeding season, many concentrate in small areas, where territories are reduced in size, and feeding grounds often shared by several pairs with no agonistic behaviour. Favourable nest-sites are occupied by many birds which gather and build their nests at short distances from one another. This occurs in the few arborescent plants of the altiplano, such as puyas (*Puya raimondii*, Bromeliaceae), and along cliffs as well.

In Tibet, birds show the same tendencies. Barheaded Geese nest in large colonies and even lay their eggs in a very promiscuous manner. Hume's Ground Jay *Pseudopodoces humilis* lives in small parties of 5-15 birds looking collectively for their food on the ground. Rednecked Snow Finches (*Montifringilla ruficollis*) do the same and Adams' Snow Finches (*M. adamsi*) even live in bands numbering up to 100 birds which display well defined social behaviour patterns. A tendency to gregariousness is found in *Grandala coelicolor*, *Acanthis flavirostris* and various representatives of the genus *Carpodacus*. Several of these birds have collective displays, which are also known in Robin Accentors, *Prunella rubiculoides*. As in the Andes, birds concentrate in the most favourable nest-sites where their density can be very high. In a small part of a cliff, nests of *Anser indicus*, *Tadorna ferruginea*, *Bubo bubo*, *Corvus corax*, *Pyrrhocorax pyrrhocorax*, *Columba rupestris*, *Gypaetus barbatus*, *Buteo hemilasius* and *Falco cherrug* were found together, the various birds living quietly side by side, though an active competition exists between birds of very distinct groups.

Rocky habitats are particularly favourable to birds. Open plateaux offer very harsh conditions to animal life, being cold and open to winds.[1] In contrast cliffs and piled boulders provide shelters against wind and snow, and the microclimate is more favourable in their vicinity. Temperatures are higher due to absence of wind and better exposure. Rock warms up quicker and better than earth when exposed to sun, and thus plays the role of a thermal regulator. As food is more abundant and as many nest-sites are available, it is no wonder that birds frequent preferably these habitats, where they nest in large numbers. In the Andes many raptors nest on small cornices along cliffs, such as caracaras (*Phalcobaenus albogularis*) and hawks (*Buteo poecilochrous*), side by side with ibises (*Theristicus branickii*), doves (*Metriopelia melanoptera*), parakeets (*Bolborhynchus aurifrons*), hummingbirds (*Oreotrochilus*) and numerous passerines, such as swallows (*Oreochelidon, Petrochelidon*), and finches (*Sicalis, Spinus*). They build their nests in crevices, sometimes under shelters and even in caves. Adaptation to rock probably opened high mountain habitats to hummingbirds. It has already been mentioned that numerous birds, mostly Fringillidae and Furnariidae, take refuge under rocks and in crevices during the night.

In Tibet too many birds became rupicoline for the same ecological reasons. Among raptors, the Tibetan Saker Falcon *Falco cherrug* nests exclusively in crags[2], in contrast to other races which nest in trees. Similar nest-sites are chosen by *Buteo hemilasius*, *Bubo bubo*, and of course *Falco tinnunculus* and *Gypaetus barbatus*. Barheaded Geese *Anser indicus* nest for a part on crags where they compete with birds of prey, often very successfully. Corvidae, such as *Corvus corax*, *Pyrrhocorax pyrrhocorax* and *P. graculus*, place their nest on crags or in a hole or fissure. Of course Wall Creepers *Tichodroma muraria* find here their optimal habitat up to 5000 m, and other passerines, Rock Sparrows *Petronia petronia* among others, nest in crevices.

Other passerines nest near the ground in hollows, or under stones and boulders. This mode of nidification is particularly adopted by representatives of the genera *Carpodacus* and *Leucosticte*, Roborovsky's Rose Finch *Kozlowia roborovskii*, some Snow Finches such as *Montifringilla adamsi*, accentors and redstarts. Their feeding grounds are located in the same habitat, where vegetal and animal food is more abundant than anywhere else.

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[1] Nevertheless open plains are not void of birds. In Peru steppes are inhabited by some passerines such as *Phrygilus alaudinus*, *Geositta cunicularia* and *Anthus correndera* in addition to various tinamous and seedsnipes (*Thinocorus orbignyianus*). In Tibet, Horned Larks *Eremophila alpestris* breed in the barest and most desolate habitats, usually in the most exposed places (Ali 1946).

[2] Since it uses old nests of ravens etc. and no tree nests are available !—SA.

The vicinity of cliffs also offers a much more favourable microclimate than the nearby areas, allowing the growth of a denser and higher vegetation of shrubs, and occasionally some small trees. Well exposed slopes are covered by dwarf scrub and stunted vegetation, which contrasts with the grassy steppe characteristic of plains and plateaux. This habitat similar to those of the temperate zone attracts a number of birds with strict ecological requirements. In the Andes such places are inhabited by hummingbirds, doves, various passerines such as *Leptasthenura andicola*, *Asthenes d'orbignyi*, *Troglodytes musculus*, *Turdus chiguanco* and *Phrygilus gayi*. In Tibet, their equivalents are *Turdus kessleri*, *Saxicola torquata*, *Phoenicurus frontalis*, *Phylloscopus affinis*, *P. fuscatus*, *Lanius sphenocercus*, *Parus superciliosus*, *Leptopoecile sophiae*, *Acanthis flavirostris*, *Emberiza cia* and *Urocynchramus pylzowi*.

Another way to escape cold and severe weather conditions is to nest in burrows. In habitats with wide daily range of temperature and a great frequency of winds with a great cooling power, detrimental to birds and particularly to their brood, this mode of nidification is highly beneficial. In the Andes, in habitats in which temperatures fluctuate daily from below 0° to 25°C, temperature within a burrow is constantly around 10°C and does not fluctuate more than 2—3°C during the whole nesting season. Birds benefit from a considerable economy of energy, highly advantageous to the young. Besides, the brood is well protected against predators. Certainly a hypogean mode of nidification is known among other birds than those of the upper zones. But it is so widespread in the high Andes and in Tibet (but not in Africa) that it can be considered as a response to the hostile conditions of this habitat.

In the Andes birds nesting underground belong to many groups, ranging from ducks (*Anas flavirostris*), doves (*Metriopelia melanoptera*), and raptors (*Falco sparverius*) to many passerines. Though some use natural cavities or holes excavated by other animals, most dig their own burrows. Andean flicker (*Colaptes rupicola*) dig long tunnels, some 1·50 m deep, in smooth earth or sand of river banks, leading to an incubation chamber, where eggs are laid on bare earth. Others, such as Furnariidae, excavate long tunnels ending in an incubation room where they accumulate vegetal matter, feathers and wool on which the eggs are laid ; some, like the ground tyrants (*Muscisaxicola*) even build a complete nest inside, the brood being thus protected at the same time by the burrow and by a cup-shaped construction.

The same mode of nesting is found among Tibetan birds, a fair proportion of which nest underground. The habit of using burrows of various rodents is a characteristic feature. Several of them live in close association and in good harmony with marmots (*Marmota bobak*) and pikas or mouse-hares (*Ochotona daurica* and allies). Little Owls *Athene noctua* nest in old marmot burrows, thus resembling the Peruvian Burrowing Owl *Speotyto cunicularia* though the latter is able to excavate its own burrow. Ruddy Shelducks always nest in cavities, sometimes among rocks, but often in marmot burrows, the nest being located up to 2 m from the entrance. With its strong incurved bill, Hume's Ground Jay (*Pseudopodoces humilis*) is able to excavate a tunnel from 30 to 180 cm deep, ending in an incubation chamber where moss, grass and wool are stored to form a very snug nest. But often it uses a pika burrow as nest site or shelter. This becomes the normal, if not the exclusive, habit of several Snow Finches (*Montifringilla taczanowskii, M. blanfordi*, and to some extent, *M. ruficollis*), which nest in pika burrows, sometimes at 3 m from the entrance, building a big nest of roots, grass and wool.

It should be remembered that underground nidification is unknown in the high mountains of Africa, in spite of the advantages it offers against the aggressive factors of the environment.

Altitudinal migrations

Though well adapted, all birds nesting in high mountains cannot survive the year round in the same habitat. When climatic conditions become too severe, many respond by altitudinal migrations. This phenomenon is known in every mountain range over the world including the temperate regions (Alps, California) where it has been studied more extensively than elsewhere. In the northern Andes, humidity is sufficient at any season to make food available to most categories of consumers which can stay permanently within the same area. In southern Peru, a very severe dry season is unfavourable to many birds, especially insectivores. It is likely that some evacuate the upper zones and descend to lower elevations where food remains available, but these movements should be limited as favourable habitats are not distant and conditions not particularly bad even in the heart of the dry season. It should also not be forgotten that permanent snow is unknown in southern Peru under 5000 m. In contrast, in the Chilean Andes, where winter is much more severe and snow may stay for long periods, altitudinal migrations are well spread among many birds, such as flamingoes, Andean Sheldgeese *Chloephaga melanoptera*, Seedsnipes *Attagis gayi* and Gay's Greyheaded Finches *Phrygilus gayi*. When winter snows set in, most descend to the valleys (Johnson 1965).

Migration is prevalent among Tibetan birds, only a few being sedentary (Vaurie 1972). Over half of the birds are true migrants and most of the others change their habitat or wander over appreciable distances to warm valleys or plains. Some, particularly seed-eaters, are only nomadic and wander on a limited scale to more favourable habitats.

Others, mostly insectivores, are true migrants. Thus *Chaimarrornis leucocephala* descend to the Indian plains. Barheaded geese evacuate their nesting grounds and winter in tropical India, reaching the south-centre of the subcontinent. Even raptors, such as *Bubo bubo*, follow the same movements, because prey is scarce in winter, as many rodents hibernate or display little activity, having stored large amounts of food (pikas, voles of the genus *Alticola*).

Thus Tibetan birds are largely migrants, in contrast to Andean birds, except those from the Chilean sector. The difference is related to the very hostile conditions which prevail in winter, much worse than in the Andes. Some even wander during summer, when weather conditions become too bad. Thus *Grandala coelicolor* gather in bands of up to 300 birds when snow-storms make the land unsuitable to them, and descend to the valleys until the weather improves. Some warblers, such as *Phylloscopus pulcher*, perform the same movements. In view of this behaviour, the breeding success of many seems very low, due to interruption of reproduction.

However some Tibetan birds do not evacuate high altitude in winter. Alpine Accentors *Prunella collaris*, tits *Parus superciliosus*, tit-warblers *Leptopoecile sophiae* and Redbreasted Rose Finches *Carpodacus puniceus* can stay all the year round in the upper zone where they have been observed in winter at an altitude of 5400 m. This represents an incredible resistance to the aggressive factors of the environment.

References

Ali, S. (1946): An ornithological pilgrimage to Lake Manasarowar and Mount Kailas. *J. Bombay nat. Hist. Soc.* **46**: 284-308.

——— (1962): The Birds of Sikkim. Madras (Oxford Univ. Press).

Dementiev, G. P., *et al.* (1966-68): Birds of the Soviet Union. Vols. 1-6. Jerusalem (Israel Program for Scientific Translations).

Dorst, J. (1956): Recherches écologiques sur les oiseaux des hauts plateaux péruviens. *Trav. Inst. Fr. Et. Andines,* **5**: 83-140.

——— (1957): The Puya stands of the Peruvian high plateaux as a bird habitat. *Ibis* **99**: 594-9.

——— (1962): A propos de la nidification hypogée de quelques oiseaux des hautes Andes péruviennes. *Oiseau Rev. Fr. Orn.* **32**: 5-14.

——— (1964): Quelques adaptations écologiques des oiseaux des hautes Andes péruviennes. *Proc. XIII Int. Orn. Congr.* (Ithaca, 1962): 658-65.

Johnson, A. W. (1965, 1967): The birds of Chile. 2 vols. Buenos Aires (Platt Est. Graf.).

Koepcke, M. (1954): Corte ecologico transversal en los Andes del Peru central con especial consideration de las aves. Parte I: Costa, Vertientes occidentales y Region altoandina. *Mem. Mus. Hist. Nat. 'Javier Prado'* 3: 1-119.

Kozlova, E. V. (1952): [Avifauna of the Tibetan highland, its relationship and history]. *Trudy Zool. Inst. Akad. Nauk. USSR,* **9**: 964-1028 (in Russian).

Ludlow, F. (1950): The birds of Lhasa. *Ibis* **92**: 34-45.

——— (1951): The birds of Kongbo and Pome, South-East Tibet. *Ibis* **93**: 547-78.

——— (1964): The birds of South-eastern Tibet. *Ibis* **86**: 43-86, 176-208, 348-89.

MOREAU, R. E. (1966): The Bird Faunas of Africa and its Islands. New York and London (Academic Press).

SCHAFER, E. (1938): Ornithologische Ergebnisse zweier Forschungsreisen nach Tibet. *J. Orn.* **86**: Suppl.

TROLL, C. (1959): Die tropischen Gebirge. *Bonner Geogr. Abhandl.* **25**: 1-93.

VAURIE, C. (1972): Tibet and its Birds. London (Witherby).

VUILLEUMIER, F. (1970): Insular biogeography in continental regions. I. The Northern Andes of South America. *Amer. Nat.* **104** (938): 373-88.

WALTON, H. J. (1906): On the birds of Southern Tibet. *Ibis* **8**(6): 57-84, 225-56.

WEIGOLD, H. (1949): Tibet einst ein Entwicklungs-zentrum. *Ornithologie als Biologische Wissenschaft*, Festschr. E. Stresemann. Heidelberg (C. Winter Universitatsverlag): 92-107.

WRIGHT, H. E., & OSBURN, W. H. (Ed.) (1967): Arctic and alpine environments. *7th Congress INOUA*, Boulder. Indianā Univ. Press.